

EVIDENCE FOR A SAND HILLS ECOTYPE OF *ESCHSCHOLZIA CALIFORNICA* (PAPAVERACEAE)

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ABSTRACT

The *Eschscholzia californica* Cham. growing in the Ben Lomond sand hills in the Santa Cruz mountains appears different from other populations in the surrounding areas. To quantify these differences, populations in coastal, sand hills, and serpentine soils were compared. Phenotypic data were collected from the field in 1998 and 1999. A common garden experiment was also performed. Differences in torus rim width, flower color, flower number, and leaf coloration were examined in both the field and the common garden. The sand hills population was different from both the coastal and the serpentine populations for leaf coloration. Population differentiation occurred among all three sites for at least some of the floral characters examined. The common garden experiment indicates that some of the differences among the populations are phenotypically stable.

INTRODUCTION

The Ben Lomond sand hills are a textbook example of the geographic factors that give rise to endemism (Mayer et al. 1994; Kruckeberg 1986). Isolated intrusions of dry sandy soil and associated drought-adapted plant communities are in stark contrast to the damp redwood forest surrounding the sand hills. Edaphic habitat disjunction can cause parapatric speciation (Kruckeberg 1954; Proctor and Wodell 1975). In the case of *Eschscholzia californica* Cham., a species that is found in open, disturbed habitats, populations in the sand hills may be isolated by large regions of dense forest habitat, eventually leading to allopatric speciation. Isolation and soil-specific adaptation can produce a great degree of population differentiation in a short period of time (Proctor and Wodell 1975).

A more common example of edaphic factors associated with endemism in the California flora is the presence of serpentine-adapted communities throughout the state. Serpentine adaptation is not treated consistently in taxonomic terms. In some cases, a serpentine-adapted group of populations is recognized as a separate subspecies (e.g., *Streptanthus insignis* Jepson ssp. *lyonii* Kruckeb. & J. Morrison) and, in other cases, it is grouped with serpentine-intolerant populations (e.g., *Streptanthus glandulosus* Hook.) (Kruckeberg 1986).

Eschscholzia californica is known for its local variation. By the early part of this century, over 90 varieties of had been described (Greene 1905). The 90 varieties were reduced to four by Munz and Keck (1968). They recognized coastal, central, southern, and dune varieties in California. *Eschscholzia californica* is known for its plasticity

and is now found in open, semi-disturbed habitats all over the globe. Cook (1961) performed a survey of *E. californica* over the state of California and found local differentiation in self-compatibility, flower fertility, seed production, and stamen number. He found a graded mosaic pattern in the distribution of nearly all the phenotypic characters he measured. Although his work focused on populations west of the Central Valley, *E. californica* in Santa Clara and Santa Cruz counties were not included. This study examines local differentiation among 3 populations in 3 different habitats in the south San Francisco Bay Area: a serpentine habitat, an inland sand hill habitat, and a coastal meadow habitat. This study looks at differentiation among the populations in two ways: field phenotypic measurement (how the plants appear in their own habitat) and common garden phenotypic measurement (controlling environmental influence). The plants at the sand hills were of particular interest due to their vibrant purple leaves with large white spots. While the species is widely recognized to be variable in terms of floral morphology and growth habit, leaf color variation has not been formally described in this species before.

Local differentiation is a much-studied phenomenon because of its contribution to evolutionary and conservation theory (Waser and Price 1985; Montagnes and Vitt 1991; Mayer et al. 1994; Kindell et al. 1996; Linhart and Grant 1996). Finding how much field-observed population differences are in response to environmental factors requires some *ex situ* investigation. Common garden experiments are effective in determining the strength of the adaptation of each population to its own soil environment. By performing a common garden experiment rather than a reciprocal transplant experiment, we focused purely on soil environment and controlled confounding factors such as unequal responses to

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differences in interspecific competition and predation that may have existed within each population. Also, by performing a common garden experiment rather than a reciprocal transplant experiment, we avoided the likelihood of polluting a possibly sensitive habitat-adapted genome (at the sand hills) with detrimental alleles.

Recognition of special, locally-adapted populations of plants has proved valuable in conservation of fragile ecosystems. Most rare plant occurrences in California are in mixed chaparral, grasslands, coastal scrub, and valley-foothill woodland, yet in terms of the percentage of total habitat preserved (wilderness areas, research reserves, national and state parks, wildlife refuges, and recreational sites) alpine and sub-alpine areas are afforded proportionally the most protection (Pavlik and Skinner 1994). While the identification of a rare plant in a previously unknown area can ensure some protection (Bartel et al. 1994), Pavlik and Skinner (1994) recommend promoting habitat-based conservation plans, particularly in serpentinite, rocky, and sandy substrates at non-alpine elevations that harbor the highest degrees of overall endemism. The sand hills are certainly a candidate for this type of protection: California Department of Fish and Game has expressed interest in this area, and 9 of the 97 species found in the sand hills are thought to be ecotypes, with 8 additional species probably warranting additional taxonomic study (Lee 1996).

METHODS

Study sites. In 1998, one coastal, one sand hills, and one serpentine population were sampled. In 1999, two coastal, two sand hills, and one serpentine population were sampled. Both coastal sites were located at Wilder Ranch State Park, just north of Santa Cruz. The sand hills sites were located in a watershed ravine just off Mt. Hermon Road in Scotts Valley. The property is privately owned and previously contained a sand quarry. The serpentine site is located on Tulare Hill in the Santa Teresa Hills in the city of San Jose. The property is leased for cattle grazing.

The coastal site sampled in both 1998 and 1999 (W1) is a tabletop meadow 0.4 km southwest of the historic ranch buildings. The site is mowed every summer, late in the flowering season. *Bromus hordeaceus* L., *Raphanus sativus* L., and *Carduus pycnocephalus* L. dominate this site. The coastal site sampled in 1999 only (W2) was located 0.4 km east of the historic ranch buildings. The species composition of this south-facing community was dominated by *Bromus diandrus* Roth and *C. pycnocephalus*. Although the sites are coastal, the *E. californica* at this location does not fit the description of the coastal "race" of *E. californica* (described in Munz and Keck 1968), but rather the inland variety. Due to the proximity of the sites to the ranch house and gardens, it is possible that these populations are descendants of once-planted individuals.

The sand hills *E. californica* population sampled in 1998 and 1999 (SH1) occurred on both the south-facing and north-facing sides of the ravine. The south-facing slope community contained a grassland understory (*Briza maxima* L. dominant) beneath scattered ponderosa pine. The north-facing slope community consisted of spring flowering annuals (*Lupinus bicolor* Lindley, *Gilia tenuiflora* Benth., *Castilleja exserta* [A. A. Helbr.] Chuang & Heckard) spread thinly over bare sand. The sand hills site sampled in 1999 only (SH2) was on the lower sloping face of a sand quarry scar 0.2 km south of the first sand hills population. The scar bends in a semi circle from south-facing to west-facing slopes. Plants at SH2 flowered 5 weeks earlier than those at SH1, and the community consisted almost entirely of *E. californica* and *Lupinus albus* Benth.

The *E. californica* population on serpentine soil (SERP) was sampled in both 1998 and 1999. The population area is located on north- and east-facing slopes in a serpentine grassland community containing species such as *Avena fatua* L., *Hordeum murinum* L. ssp. *leporinum* and *Lasthenia platyglossa*.

Populations located on the same soil type were close enough together that gene flow between them is a distinct possibility. Differences in plant community composition and extremely low densities of *E. californica* plants between the populations indicated that separate treatment might be appropriate. In all cases, the entire population of *E. californica* was not measured, but rather a high-density lobe within the population was sampled. Individual plants of *E. californica* could be found at low densities for thousands of meters from the sampling areas. Sampling areas were defined by high *E. californica* concentration (generally more than 1 plant per m²), and also by artificial (fences, drainage ditches) and geologic (cliffs and other drastic changes in slope) barriers.

Field data collection. In 1998, 3 populations were sampled for plant phenotypic characteristics. Population W1 was sampled on June 26; SERP was sampled on May 1; SH1 was sampled on July 1. An effort was made to sample each population when the largest numbers of plants were flowering. Between 45 and 65 plants were randomly sampled at each population. Data collected for each plant were the number of floral units, leaf color, torus rim width, and flower 1-color or bicolor. Floral units were recorded as the number of flowers plus the number of buds plus the number of capsules. Torus rim width and flower color were measured on the tallest flower. Torus rim width was taken at the widest point and was recorded as either 1, 2, or 3 mm.

Flower color was recorded by comparing the base to the tip of the petals on the flower on the tallest branch. Obvious differences between the two were considered to be evidence of the "bicolor"

character in the flower. If there appeared to be only a slight difference between the color of the tip of the petal compared to the base of the petal, or no difference at all, the flower was recorded as "1-color."

Leaf color data were collected by observing the color characteristics of the leaf: presence of white spots, visible presence of green pigmentation, visible presence of purple pigmentation, and presence of red tips on the leaf. Red-tipped leaves appear to be fairly common in *E. californica*, and almost all living leaves of the plant can be characterized as green. However, some leaves of *E. californica* have a purplish tinge that is found throughout the leaf. Where green was visible and tinged with purple, both the green leaved and the purple leaved character were marked as present. In some plants this purple color is so vibrant that no green color can be seen. In these plants, the purple-leaf character was recorded as present, and the green-leaf character was recorded as absent. In 1998, each character was noted as either present or absent for the third leaf from the top of the longest branch of each randomly selected plant.

Stanton Cook (1961) used flower color and torus rim width in his investigations of statewide variability in *E. californica*. Clark and Charest (1992) used number of floral units in their study of population differentiation in the Antelope Valley. Leaf color was of interest because of the apparent difference between the sand hills population for this character and the other two populations.

In 1999, 15 plants per population were sampled for floral characters to see if the differences observed among populations were consistent and if they would be present in two very different climatic years: El Niño and La Niña winters (NOAA 2000). Number of flower units, torus rim width and flower color were measured over time at sites W1, SH1, and SERP to make sure that differences observed in 1998 would be consistent within the season. Fifteen plants were sampled in each population every 2 weeks. The same sampling scheme was used for each data collection. Although it is unlikely that the same plants were measured on each sampling date, the plants were located in roughly the same areas. Sampling dates were April 1, April 15, April 28, May 12, May 27, and June 10.

Floral and leaf character data were collected at the estimated peak of flowering for W1 (April 15), W2 (May 13), SH1 (May 27), SH2 (April 22), and SERP (April 28). Instead of just looking at a single leaf of the plant, all of the leaves of the plant were examined for leaf color characters in 1999. Because no differences were found for this character in 1998, data on the red-tipped leaf character were not collected in 1999.

Common garden experiment. Seeds were collected from W1 and SH1 in July 1998 from 30 randomly selected plants in each population. The

TABLE 1. DESIGN OF THE COMMON GARDEN EXPERIMENT.

Soil source	Seed source	# pots	# seeds/pot
SH1	SH1	16	9
W1	SH1	16	9
SH1	W1	11	6
W1	W1	11	6

seeds, identified by parent plant, were stored in paper envelopes until February 1999, at which time the seeds were placed in 10 cm × 10 cm pots filled with soil from the W1 and SH1 population areas. Only ripe seeds were used; collected seeds that were unripe were not used in the experiment. A total of 210 seeds from 11 plants from SH1 and 210 seeds from 6 plants from W1 were used in the experiment. In all but 2 pots, seeds from only 1 parent were sown per pot. Due to seed from some SH parents not germinating, common garden data were collected from progeny of 8 (out of 11) SH parents and all 6 W parents.

Soil was collected from locations near, but not within the SH1 and W1 populations. This limited the possibility of contamination with seed from population seed banks. In order to identify whether contamination occurred despite our efforts, seeds were planted in an X-shaped pattern in each pot. Soil was collected within a week of seed potting to minimize biotic changes in the soil that might occur as a result of storage method. Neither SERP soil nor SERP seed was used in the common garden experiment because of the lack of differentiation of this population from the W1 population in the 1998 results.

A reciprocal planting design allowed for seed from each population to be planted in its own and the other's soil (Table 1). Each pot was labeled with a unique 3-digit randomly generated number to prevent bias when measuring plant characters. Recorded measurements were matched to the plant parent population only at the completion of the experiment.

A wick-based watering system was used, where the pots were placed on moist quilt batting dipped in tap water. This kept the flow of water to the base of the pots consistent, and pots were able to take up as much water as was transpired or evaporated. No extra fertilization was used. The pots were placed on the rooftop of Duncan Hall at SJSU for the months of February through April. In late April, the rooftop was so hot and sunny that the watering system was unable to keep up with the plants' water needs without daily attention. The pots were moved to a northwest-facing patio in Pacifica for the remainder of the experiment.

Germination and leaf color were monitored on a weekly basis. Pots were thinned to one plant per pot by retaining the plant growing closest to the center of the pot. In cases where several plants were

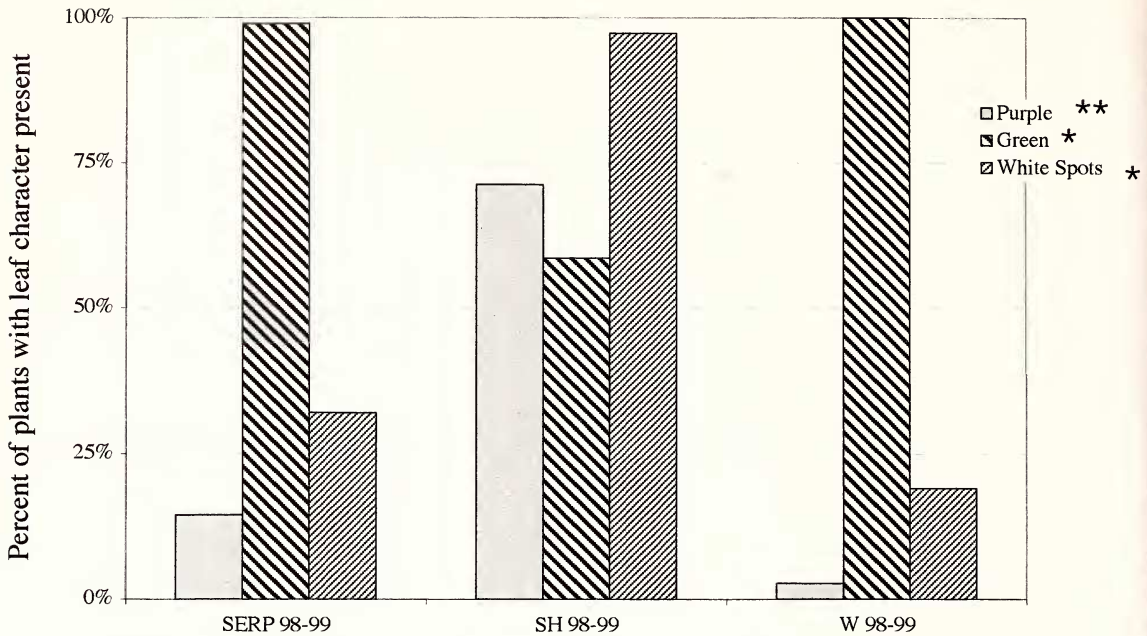


FIG. 1. Percent presence of leaf characters for all populations, 1998 and 1999 combined. *SH populations different from W and SERP populations ($P < 0.01$). **All 3 soil types different from each other ($P < 0.01$).

equidistant from the center of the pot, the largest plant was kept. Leaf color data were collected from all the leaves of each plant. When plants flowered, torus rim width data were collected from all flowers.

Data analysis. The majority of statistical tests were performed in SAS (1990 Ver. 6.0) using the general linear model. G-fit tests performed in Microsoft Excel (1998 Ver 7.0) were used to test for differences among populations in frequencies of discrete characters (Sprinthall 1987). Discrete character frequencies were normalized before analysis. The Bonferroni correction was used in deciding the critical value (adjusted from $\alpha = 0.05$) to minimize the risk of coming upon a chance difference between populations because of the number of characters being compared. A repeated measures MANOVA (SYSTAT 1992 Ver. 5.2.1) was used to define differences over time in 1999 data for torus rim width and number of floral units per plant. All percentage data were arcsine transformed prior to analysis.

RESULTS

Field data collection. To show the total variability in expression of leaf color characters in 2 very different climatic years, leaf color data was combined over 1998 and 1999 for analysis. All 3 populations differed from each other in the purple-leaf character. Purple leaves were much more prevalent in SH populations than in either the SERP or W populations (Fig. 1), but the SERP population had significantly higher number of leaves with purple

than the W populations ($P < 0.01$). All plants at SERP and W sites in both years had leaves with visible green, but many plants at SH sites lacked visible green pigment. Almost all plants at SH sites had white-spotted leaves, but less than a third of plants at the other sites had this leaf coloration character. While SERP and W populations were similar for green-leaf and white-spotted-leaf characters, SH populations were different from both for these characters ($P < 0.01$). No differences were found in the distribution of the red-tipped leaf character in 1998.

Differences in floral characteristics were found among populations in 1998 (Table 2). The torus rim was much narrower in the SH populations than in the W and SERP populations ($P < 0.01$). The bicolor flower character was less prevalent in the SH population in 1998 than in the other two populations ($P < 0.01$). In 1998, SH sites also tended to have more floral units than the other two site types ($P < 0.01$).

Floral measurements were taken over time in 1999 to test the validity of a single-date sampling scheme in 1998. If the characters changed over time, differences observed in 1998 could be attributed to the date of sampling. No differences were found in torus rim width over time ($P = 0.14$). There was a statistical interaction between measurement date and population site for the bicolor flower character ($P < 0.002$, Fig. 2): the number of bicolor flowers increased over time in the SERP population ($P < 0.01$), but remained about the same in the other two populations, although the dip in

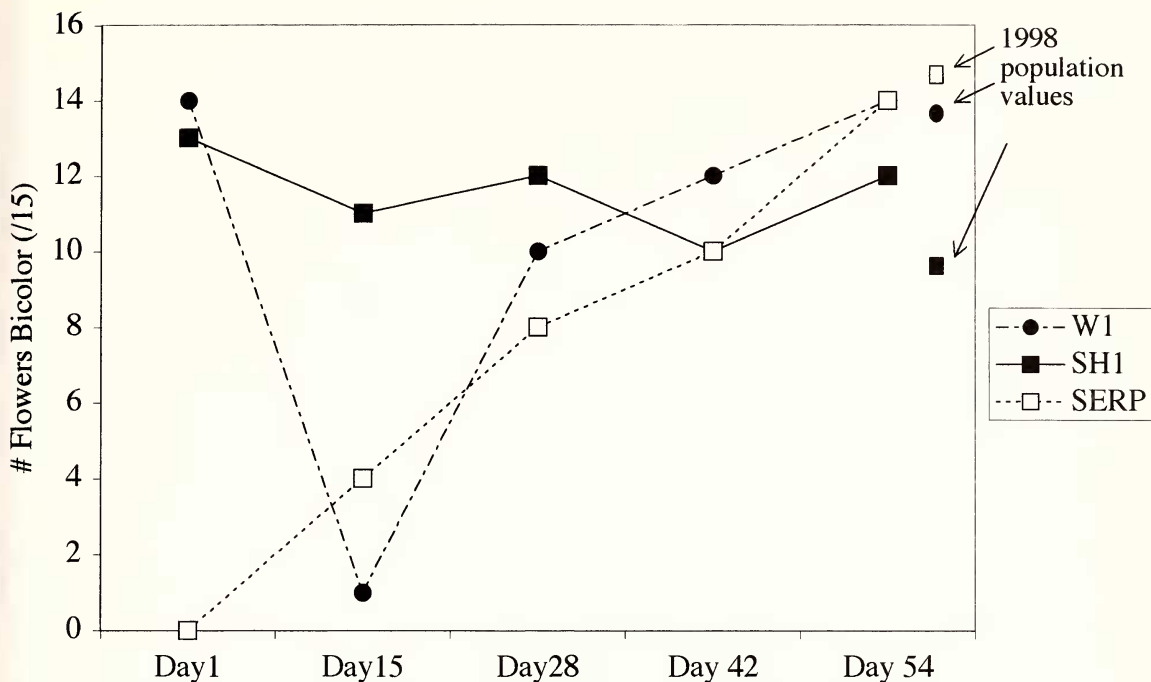


FIG. 2. Number of bicolor flowers ($n = 15$) for W1, SH1, and SERP populations over time in 1999. Normalized values from 1998 are included. Change over time significantly different among all 3 populations ($P < 0.01$).

the W population in week 2 is not a random effect ($P < 0.01$). The number of floral units per plant increased over time in all populations, but increased more slowly in the SERP population versus the other two populations (Fig. 3).

Since torus rim width did not change over time in 1999, all collection dates and years were lumped to confirm the differences among populations. There was a year by site statistical interaction for this character ($P < 0.0001$). Torus rims were larger in 1999 compared to 1998, but the populations kept their size difference relative to each other: SH rims were the smallest, W rims were the largest, and SERP rims were intermediate (Table 2).

Common garden experiment. No *E. californica* germinated outside the X-shaped seed planting pattern. This does not prove the soil was uncontaminated with an existing seed bank, but such contamination is unlikely. Leaf phenotype remained constant throughout the experiment: once true leaves emerged, they did not change color over time. All SH progeny had purple leaves, regardless of the soil type in which they were grown (Fig. 4). Two W progeny had purple leaves when grown in SH soil, but this distribution was not very different from W in the field. Green leaves were more often absent from SH progeny, again regardless of soil type. All SH progeny had white-spotted leaves, regardless of soil type, where this character was only sometimes present in W progeny.

All plants planted in W soil flowered, regardless

of parent type, but only 7 of the 11 SH plants flowered in their own soil, and only 1 of the 7 W plants flowered in SH soil. Torus rim width (Table 3) is influenced by parent population ($P < 0.001$), individual parent plant ($P < 0.001$), and soil type ($P < 0.0162$): rim width for SH plants was less than for W plants in both soil types, however, torus rims from both parent sources were smaller in SH soil compared to W soil.

DISCUSSION

The differences observed between the populations in terms of the bicolor characteristic and the number of floral units in 1998 were due to the single-date sampling scheme. As shown from the 1999 data, the populations do differ in their expression of these traits, but with the single-date sampling scheme in 1998, lack of difference could just as easily have been observed. This change in some traits over time should serve as a cautionary note to other researchers who plan to sample populations only once per year. The change in flower color and number of floral units over time is not a similarly-expressed trait: the type of change over time varies among populations. It is difficult to say what affects this change over time in some populations but not others. Different types of drying patterns and different soil chemistries at the population sites could be responsible, or these differences could be due to differential responses among the populations to the same environmental factors. Since *E. californica* is

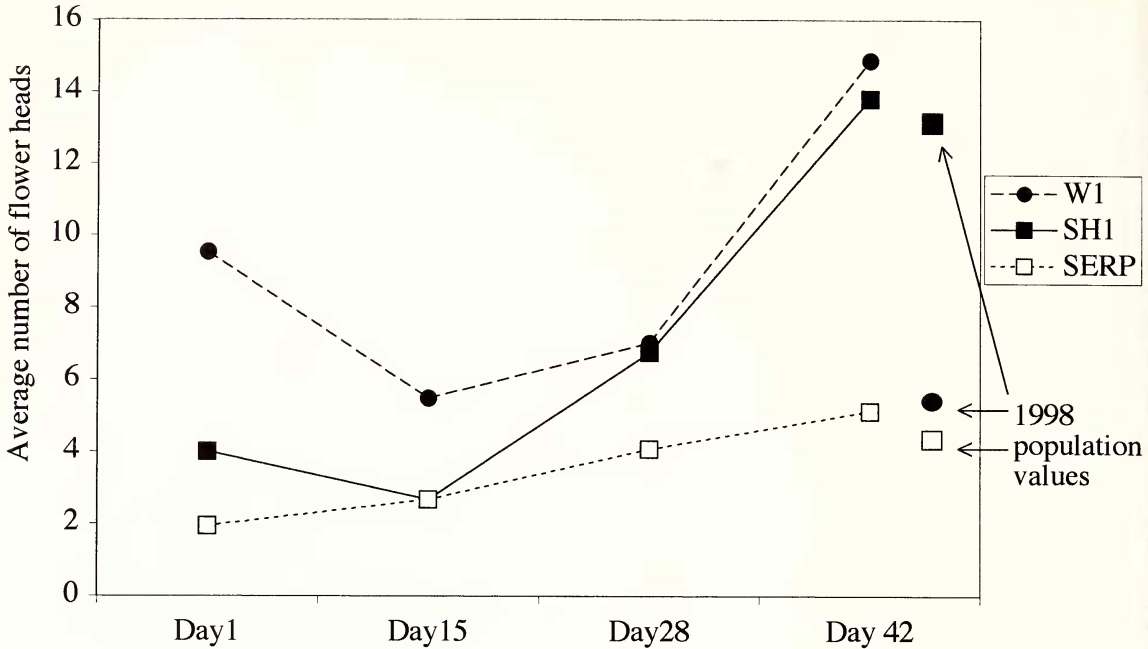


FIG. 3. Average number of flowers per plant for W1, SH1, and SERP populations over time in 1999. Single values from 1998 are included. Change over time significantly different among all 3 populations ($P < 0.01$).

a plant that has an indeterminate flowering system, the dip seen at Day 15 in number of floral units in W and SH populations is puzzling. We would expect the number of floral units to increase throughout the season. It is possible that a subpopulation of early-flowering plants was sampled at Day 1 and that Day 15 represented the start of the season for a later-flowering subpopulation.

Torus rim width does not appear to change over the flowering season and differences observed between the populations in 1998 were confirmed when the data for the two years were analyzed together. Torus rim width did change between years, and while this indicates some plasticity for this character, it also indicates that the variability is constrained differently within each population.

In the common garden experiment, SH plants kept their purple and white coloration even when planted in Wilder Ranch soil. All SH plants had purple and white coloration even though, while the expression of white coloration is close to 100% in

the field, the expression of purple coloration in the field is lower. Progeny from only 8 SH plants were used in the common garden experiment, so it is likely that this difference between common garden and field is due to small sample size. It is clear that the expression of leaf coloration characters that contribute to population differentiation in *E. californica* is phenotypically stable. The purple-leaf, white-spotted characteristic of sand hills plant leaves does not appear to be a direct response to soil type. Although the differences in leaf color are phenotypically stable, they may not be genetic. Effects of the maternal environment in which the seed ripens have been known to include everything from seed germination rates to progeny plants' tolerance to saline environments (see Rossiter 1995 for review). Although leaf color in particular has not been shown to be determined by maternal environment, seed gathered from controlled pollinations of the potted plants should be grown to determine the

TABLE 2. FLORAL CHARACTERISTICS. All averages ± 1 SD. ¹ For 1998 and 1999 data combined, both populations from each soil type were included. ^{a,b,c} For each row, values with different letters are statistically different ($P < 0.01$).

	W ¹	SH ¹	SERP
# floral units 1998	5.90 \pm 5.05 ^a	12.78 \pm 15.9 ^b	4.15 \pm 3.27 ^a
% big color 1998	92.0 ^a	65.3 ^b	95.5 ^a
Torus rim (mm) 1998	1.42 \pm 0.7 ^a	1.04 \pm 0.2 ^b	1.41 \pm 0.06 ^a
1998 and 1999 combined	2.34 \pm 1.04 ^a	1.14 \pm 0.47 ^b	1.52 \pm 0.62 ^c
1998	n = 50	n = 49	n = 66
1998 and 1998	n = 141	n = 142	n = 143

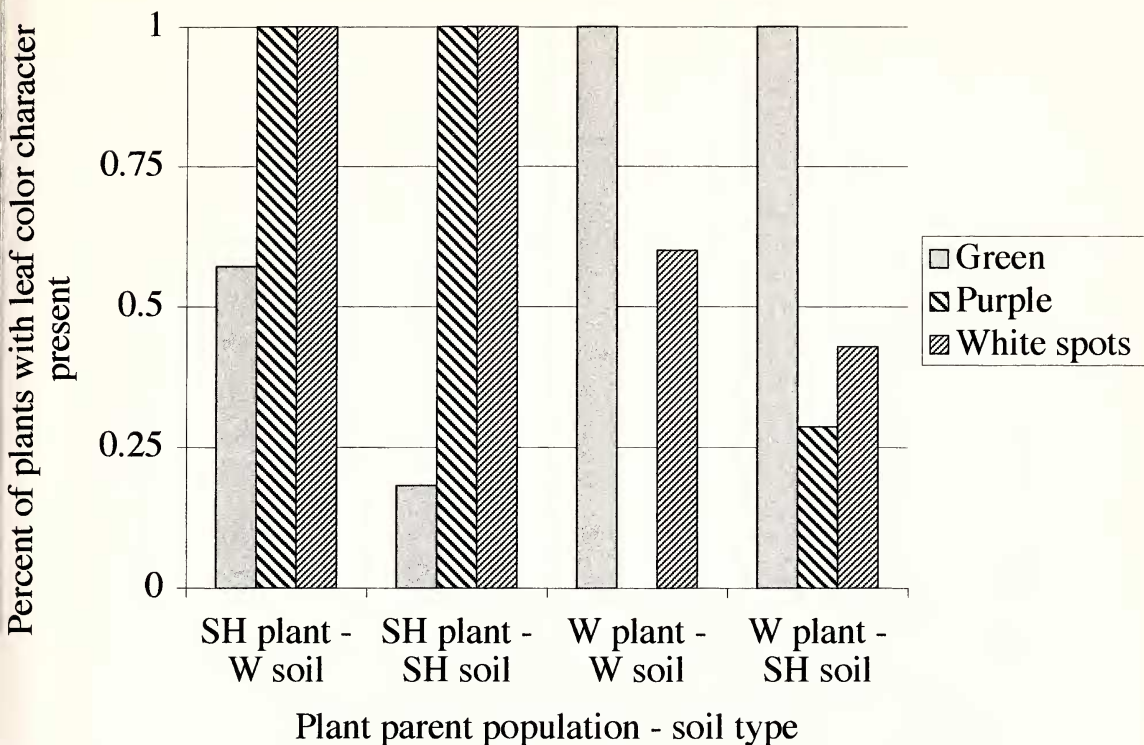


FIG. 4. Leaf color characteristics in the common garden experiment.

strength of any effects of maternal environment upon leaf phenotype.

Population differentiation is a relatively common phenomenon, but differentiation among populations is expected to be less strong when the flowers are large and the plants outcross than when the flowers are small and the plants are autogamous (Linhart and Grant 1996). Floral characteristics are less likely to be divergent among populations than vegetative ones (Slentz et al. 1999), as usually even the most disparate populations still have the same pollinator species, and thus floral characters tend to be uniformly selected. On the other hand, the characters measured in this study may not be undergoing selection at all.

While a few leaves with purple coloration and white spots were found at W and SERP locations, no plants at these locations had the vibrant purple

coloration masking the visibility of green pigments in their leaves. The sand hills are host to many endemic species (Lee 1996), probably adapted to the particular edaphic environment. The phenotypic stability of leaf-color differences and the influence of parent population on torus rim width indicate that the sand hills population is probably genetically differentiated from the other two populations in this study. Proximate causes of this differentiation are still a mystery: is this differentiation maintained by lack of gene flow into the population, or solely by strong selective forces at the population site?

Even though *E. californica* is a near-obligate outbreeder, pollinated by insects and wind which can carry pollen over a considerable range, Cook (1961) found that *E. californica* populations can be differentiated in as small a scale as hundreds of feet. Differentiation has also been found at distances of less than 3 km (Clark and Charest 1992). The balance between phenotypic plasticity and differential adaptation is not known in this species. Both Cook's and Clark and Charest's results were from field observations: only self-compatibility was tested in a common garden experiment by Cook. It is certainly possible that the species is not as plastic as once thought (i.e., the same genes reacting differently to different environments), but instead adapts locally (different genes in different environments) to exhibit the great variety we observe. A

TABLE 3. TORUS RIM WIDTH IN COMMON GARDEN EXPERIMENT BY PARENT POPULATION AND SOIL TYPE. All averages ± 1 SD.

Parent population	Soil type	Torus rim width (mm)	Total
SH	W	1.07 \pm 0.53	7
SH	SH	0.54 \pm 0.48	7
W	W	2.91 \pm 0.79	5
W	SH	2.00	1

confounding factor to further investigation of local adaptation is the widespread use of *E. californica* cultivars in landscaping and the success of the species at colonization. Future studies may wish to attempt to determine the extent of cultivar introgression for older populations (Clark and Charest 1992).

This study was designed to determine if the populations at the sand hills at the very least represent an ecotype of the *E. californica* species (*sensu* Toresson 1922 and Kruckeberg 1951). A sand hills ecotype may be indicated by these results. Testing the interfertility of sand hills with surrounding populations and examining the possibility and efficacy of gene flow to the sand hills population will give more information on how the leaf coloration of the *E. californica* at the sand hills is maintained.

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